ELSEVIER

Cognitive Brain Research 13 (2002) 203–212

COGNITIVE BRAIN RESEARCH

www.elsevier.com/locate/bres

Research report

Spatial imagery in deductive reasoning: a functional MRI study

Markus Knauff[a,*], Thomas Mulack[a,b], Jan Kassubek[b], Helmut R. Salih[c], Mark W. Greenlee[d]

[a]*Center for Cognitive Science, University of Freiburg, Friedrichstr. 50, 79098 Freiburg, Germany*
[b]*Department of Neurology, University Hospital of Freiburg, Freiburg, Germany*
[c]*Department of Medicine, University Hospital of Tübingen, Tübingen, Germany*
[d]*Department of Psychology, University of Oldenburg, Oldenburg, Germany*

Accepted 17 October 2001

Abstract

Various cognitive theories aim to explain human deductive reasoning: (1) mental logic theories claim syntactic language-based proofs of derivation, (2) the mental model theory proposes cognitive processes of constructing and manipulating spatially organized mental models, and (3) imagery theories postulate that such abilities are based on visual mental images. To explore the neural substrates of human deductive reasoning, we examined BOLD (blood oxygen level dependent) contrasts of twelve healthy participants during relational and conditional reasoning with whole-brain functional magnetic resonance imaging (fMRI). The results indicate that, in the absence of any correlated visual input, reasoning activated an occipitoparietal–frontal network, including parts of the prefrontal cortex (Brodmann's area, BA, 6, 9) and the cingulate gyrus (BA 32), the superior and inferior parietal cortex (BA 7, 40), the precuneus (BA 7), and the visual association cortex (BA 19). In the discussion, we first focus on the activated occipito-parietal pathway that is well known to be involved in spatial perception and spatial working memory. Second, we briefly relate the activation in the prefrontal cortical areas and in the anterior cingulate gyrus to other imaging studies on higher cognitive functions. Finally, we draw some general conclusions and argue that reasoners envisage and inspect spatially organized mental models to solve deductive inference problems.

Theme: Neural basis of behavior

Topic: Cognition

Keywords: Reasoning; Deduction; Mental imagery; Spatial mental model; Parieto-occipital pathway; fMRI

1. Introduction

Reasoning is a cognitive process that yields conclusions from given premises. It occurs whenever human beings make implicit information explicit. This study is about one form of reasoning, deduction. By definition, in deductive reasoning, the truth of the premises ensures the truth of the conclusion. (In contrast to inductive reasoning, in which the truth of the premises does not warrant the truth of the conclusion.)

Many people report that they often think by visualizing objects and events. They typically experience reasoning as seeing the information from the premises and scanning this vivid mental image to find new, not explicitly given information. Various sorts of evidence are compatible with this assumption, including the well-known studies of the mental rotation and the mental scanning of images [40,60].

However, in the behavioral sciences, the question of how people reason deductively is still open. Cognitive psychologists conducted behavioral experiments to investigate the cognitive processes underlying different kinds of deduction, such as conditional reasoning, syllogistic reasoning, relational reasoning, etc. Nevertheless, there is still controversy on how the experimental findings can be integrated into a general theory of human reasoning. Mental proof theories completely deny that reasoning is based on mental imagery, but rather on the application of language-like formal rules of inference [6,55]. In contrast, the mental model theory postulates that reasoning does not rely on syntactic operations as in rule-based approaches, but rather on the construction and manipulation of spatially organized mental models [19,29]. Such mental models

*Corresponding author. Tel.: +49-761-203-4944; fax: +49-761-203-4938.

E-mail address: knauff@cognition.iig.uni-freiburg.de (M. Knauff).

0926-6410/02/$ – see front matter
PII: S0926-6410(01)00116-1

represent situations spatially, but they can abstract away from visual details such as colors, textures, and shapes, which are not relevant to the problem.

The third approach is the visual mental imagery theory. Proponents of this account describe mental images used in reasoning as structurally similar to perceptions. Like visual precepts, visual mental images represent colors, shapes, and metrical distance, can be rotated and scanned, have a limited resolution [14,40], and sometimes are so similar to real perceptions that the two can be confused [25]. Reasoning, from this point of view, is to 'look' mentally at a visual mental image to find new information not explicitly given in the premises.

The notion of spatial mental models and visual mental images is related to Kosslyn's model in which mental imagery is composed of two different kinds of processes, one visual and one spatial [41]. The latter is concerned with what an image looks like from a certain point of view; the former depends on where an object is located relative to other objects. The role of visual mental images and spatial mental models in deductive reasoning has been studied extensively, for instance, in Refs. [33,34].

All three cognitive approaches have been implemented in computational models. Hagert [24], for instance, proposed a computational account of relational reasoning that is based on the application of formal inference rules. Schlieder [58] implemented relational reasoning as the construction and inspection of spatial mental models [23]. A computational approach of visual mental imagery in reasoning has been developed by Glasgow and Papadias [21]. Further computational visual imagery approaches can be found in Glasgow et al. [22]. A comparison of spatial mental models and visual mental imagery in reasoning is given in Schlieder and Berendt [59].

In recent years, the debate within cognitive and computational theories of reasoning regarding sentential mental proofs, spatial mental models, and visual mental images also started in the cognitive neurosciences. On the neuroanatomical level, the sentential theory predicts that the language processing regions of the brain are involved in reasoning, whereas the spatial theory predicts that the cortical areas involved in spatial working memory, perception, and movement control are evoked by reasoning. The sentential theory, furthermore, predicts a dominance of the left hemisphere, whereas the spatial theory assumes a right hemispheric prevalence [19,20,27]. According to the visual theory, the primary visual cortex, or at least nearby visual regions, should be evoked by reasoning without a specific assumption concerning hemispheric differences [41].

While past studies on the neural basis of human reasoning were restricted to investigations with brain damaged patients [7,9,16,17,51,54], more recent neuroimaging techniques, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), were used to study reasoning processes in the intact brain. However, the results of these studies are contradicting. On the one hand, Goel et al. [19,20] investigated deductive (and inductive) reasoning problems in two PET studies and reported activation in temporal and prefrontal regions, mainly in the left hemisphere. These results appear to support the sentential theory. On the other hand, there are results that at least indirectly support the spatial and visual theories of reasoning. Prabhakaran et al. [53] studied problems selected from the Raven's Progressive Matrices Test, which elicit reasoning, and found increased activity in right frontal and bilateral parietal regions. Osherson et al. [48] compared probabilistic and deductive thinking and found in the latter increased activation in right-hemisphere parietal regions. The visual theory is related to a series of studies that found activity in the primary visual cortex when participants manipulated objects and scenes in working memory [42–44,57].

The aim of the present fMRI study is to explore the neural substrates of human deductive reasoning, and specifically, its visual and spatial components. We selected two essential sorts of human deductive reasoning: relational and conditional reasoning. In a typical relational reasoning problem, at least two relational terms $X\ r_1\ Y$ and $Y\ r_2\ Z$ are given as premises, and the goal is to find a conclusion $X\ r_3\ Z$ that follows from the premises. In a conditional reasoning problem, the first premise consists of an 'if *p*, then *q*' statement and the second premise refers to the truth of the antecedent ('if' part) or the consequent ('then' part). The goal is to find a conclusion that follows from both premises. The two valid inferences are 'if *p*, then *q*, and *p* is true, then *q* is true' (modus ponens), and 'if *p*, then *q*, and *q* is false, then *p* is false' (modus tollens).

2. Method

2.1. Participants

Twelve right-handed male students of Freiburg University (mean age = 23.9, S.D. = 3.3) participated in the experiment. None had any history of neurological or psychiatric disorders. They were paid for their participation and informed consent was obtained in writing. Before the brain imaging study started, participants attended a 20-min training experiment in which they solved 12 conditional and 12 relational sample reasoning tasks. Participants were not instructed in any way to choose a particular reasoning strategy.

2.2. Design and materials

The materials consisted of relational and conditional reasoning problems. The participants acted as their own controls and evaluated six valid and six invalid inferences of the two types of reasoning, making a total of 24 problems. The relational inferences included the following relations: left of, right of, overlaps from the left, overlaps

from the right, meets from the left, meets from the right, inside, and outside. These spatial–relational expressions have been used successfully in earlier experiments [32,39]. The inferences had the following form:

> The red rectangle is to the left of the green rectangle.
> The green rectangle overlaps the blue rectangle from the left.
> Does it follow:
> The red rectangle is to the left of the blue rectangle?

In the conditional problems, half of the inferences were in the form of modus ponens and the other half in the form of modus tollens. The inferences included expressions such as: hates, loves, bores, offends. Here is an example of an inference with a valid conclusion:

> If the man is in love, then he likes pizza.
> The man is in love.
> Does it follow:
> The man likes pizza?

Tasks were presented verbally via pneumatic headphones and, except for a tiny fixation cross, there was no further visual input. Problems were presented with a volume that participants had chosen at the beginning of the experiment. All sentences of the reasoning problems were audiotaped, grammatically correct, and were of roughly equal length.

2.3. Procedure

The experiment consisted of two experimental runs, and each run of three blocks: (1) relational reasoning, (2) conditional reasoning, and (3) fixation of a cross on neutral background (baseline condition). Each experimental run lasted about 12 min. Six relational problems were presented in each of both relational (1) and conditional (2) blocks.

Premises and conclusions of both sorts of problems were each 5 s long and were interleaved by a 5-s blank period. During the blank period after the conclusion, participants had to decide whether or not the conclusion logically follows the premises by pressing associated buttons on a response box they held in hand.

The fixation cross was projected onto a rear-projection screen covering the rear end of the scanner bore by an LCD projector. The participants were instructed to keep their eyes open at all times and to fixate the central cross to minimize eye movements. They wore headphones and were positioned with their heads in a radio-frequency transmit–receive full headcoil, looking up into a mirror in which the fixation cross of the projection screen was reflected. Head motion was minimized with a vacuum cap, which was secured within the head coil. Task presentation was synchronized to the image acquisition procedure. This was achieved by means of a pulse generated by the tomograph, which controlled the computer. Scanning took place in the blank period directly after the auditory presentations of the stimuli (premises and conclusions). The sequence of conditions was counterbalanced over participants and the order of problems under each condition was randomized.

2.4. fMRI data acquisition

Local variations in blood oxygenation level dependent (BOLD) response were measured on a 1.5-T Vision scanner (Siemens) using susceptibility-based functional magnetic resonance imaging, applying gradient-recalled echo-planar imaging (EPI) sequences. Twenty-four parallel 4-mm thick planes, positioned slightly oblique to the axial plane and covering the whole brain were imaged using a T2*-weighted sequence (TR 10 s, TE 66 ms, FA 90°, matrix 256×256 mm, voxel 2×2×4 mm). Sagittal T1-weighted magnetization-prepared rapid-acquisition gradient echo (MP-RAGE) images of the entire brain (160 slices) were acquired for anatomical localization of functional responses (TR 40 ms, TE 6 ms, FA 40°, matrix 256×256 mm, voxel size 1×1×1 mm). Statistical maps were transformed to the same resolution as the 3-D MR data set by interpolation.

2.5. Data analysis and statistics

The T1-weighted image data were used to determine the anatomical localization of functional responses. Each individual brain was scaled linearly to match the Talairach atlas [65], and Talairach coordinates are reported for the center of each region of interest (ROI). The data were analyzed and visualized using the BrainTools software [61]. Residual head motion caused some image misalignment, which was corrected by the 2-D motion correction program IMREG that is part of the AFNI package [8]. It aligns each image in the time series to the average image position. The motion-corrected data were then analyzed using a correlation method based on methods established by Bandettini et al. [4] and Friston et al. [15]. The time course of the BOLD response profile was correlated with the on/off cycle of stimulation. To reduce noise, spatial smoothing of the functional signal within each slice was performed by convolution with a 2-D Gaussian function [15] having a standard deviation of 1.7 mm. The time course of each voxel was correlated with a smoothed squarewave convolved with a Gaussian function (time constant = 4 s) [15].

Functional activation images were constructed as pseudo-color overlays on the corresponding T1-weighted anatomical slices. Only voxels with correlation coefficients greater than 0.5 ($P_{voxel} < 0.001$ where P_{voxel} = probability of a false positive, per voxel) were visualized. The

correlation values were then normalized to a *Z*-score statistics. Responses in selected ROIs were statistically analyzed to determine the relative magnitude of activation across different stimulus conditions. Voxel clusters containing a minimum of 8×8 contiguous voxels were selected, and for the contrasts only ROIs were investigated in which more than 50% of the subjects showed significant differences of activation. Analysis of variance with repeated measurements was performed on the results of BOLD responses in all ROIs. The activation level was indexed by the standard deviation of the T2* signal. To weight this activation by the extent to which it is correlated with the stimulus time course, we multiplied the response by the standardized correlation coefficient [61]. Additional statistical analysis (ANOVA for repeated measurements) was performed on the ROI data using SPSS. *Z*-scores of the functional activation were calculated from correlation values, activation amplitudes, and estimated degrees of freedom, separated for hemispheres and Brodmann's areas. Further details of data processing can be found in previous publications of the group [30].

3. Results

3.1. Behavioral data

Overall, participants' performance in the behavioral experiment was slightly better (86.7% correct) than inside the scanner (81.9% correct). However, since the patterns of results were identical outside and inside the scanner, in the following we report only data from the scanning. The analysis of response latencies shows that participants needed the same time for correct responses in the relational inferences (2.0 s) and the conditional problems (2.1 s) (*t*-test, $t=1.074$; $P>0.285$) and for modus ponens (2.1 s) and modus tollens (2.1 s) problems (*t*-test; $t=0.216$; $P>0.83$). The analysis of correct responses did not yield a reliable difference in accuracy for relational (78.8% correct) and conditional (85.2% correct) reasoning (Wilcoxon test $Z=1.8$; $P>0.67$), but the comparison of conditional problems shows that participants gave significantly more correct answers to problems in the form of modus ponens (93.3% correct) than in the form of modus tollens (79.4% correct) (Wilcoxon test $Z=1.97$; $P<0.047$). These data are in line with other experiments in which the number of correct responses for the relational problems was in the same range [38,39], and with studies showing that problems in the form of modus tollens are harder than those in the form of modus ponens [13].

3.2. Functional imaging data

In the following, we report the results for all regions of interest (ROIs) that revealed a statistically significant increase of activity in at least one of the three contrasts: (1) conditional reasoning vs. baseline, (2) relational reasoning vs. baseline, and (3) conditional vs. relational reasoning.

Since the tasks were presented verbally, it is not surprising that during both kinds of reasoning, the largest increase of activity was found in the primary auditory cortex (BA 41, 42; *Z*-scores>4). These regions were eliminated from the further analysis.

The conditional problems (conditional vs. baseline) and the relational problems (relational vs. baseline) resulted in activity in the prefrontal cortex, where significant activity was found bilaterally in the medial frontal gyrus, functionally corresponding to the supplementary motor area (SMA; part of BA 6), the middle frontal gyrus (BA 9), and a portion of the cingulate gyrus (BA 32).

In the temporal cortex, significant activation was observed bilaterally in the middle temporal gyrus (BA 21, 22). In the parietal cortex, a significant increase of activation occurred bilaterally in inferior (BA 40) and superior regions and the precuneus (both BA 7). Occipital activation was found in the visual association cortex (BA 19), but not in the primary visual cortex. The mean activities in the relevant ROIs for the contrasts conditional vs. baseline and relational vs. baseline are depicted in Fig. 1a and b, respectively. Fig. 2 illustrates representative axial and coronal slices of one subject showing localization of activated ROIs in prefrontal (BA 9) and parietal areas (BA 7) superimposed on an anatomical MRI data set.

We also directly compared the two sorts of reasoning. This comparison (conditional vs. relational) yielded activity that was greater for relational than for conditional reasoning. Bilateral increased activity was obtained in the medial frontal gyrus (BA6), the superior parietal gyrus and the precuneus, the inferior parietal cortex (BA 40), and the extrastriate cortex (BA 19). The activated ROIs (anatomical localization and Brodmann's area together with mean Talairach coordinates, separated for the left and right hemisphere) and mean *Z*-scores in the three contrasts are summarized in Table 1.

4. Discussion

The reported results can be summarized under two headlines. First, we focus on the most striking result of the present study, namely that reasoning activated the occipito-parietal pathway in the absence of any correlated visual input. Second, we briefly relate the activation in the prefrontal cortical areas and in the anterior cingulate gyrus to other imaging studies on higher cognitive functions. Finally, we draw some general conclusions an spatial mental models, visual imagery, and reasoning.

4.1. Parietal and occipital activation

The most important result of the present study is that

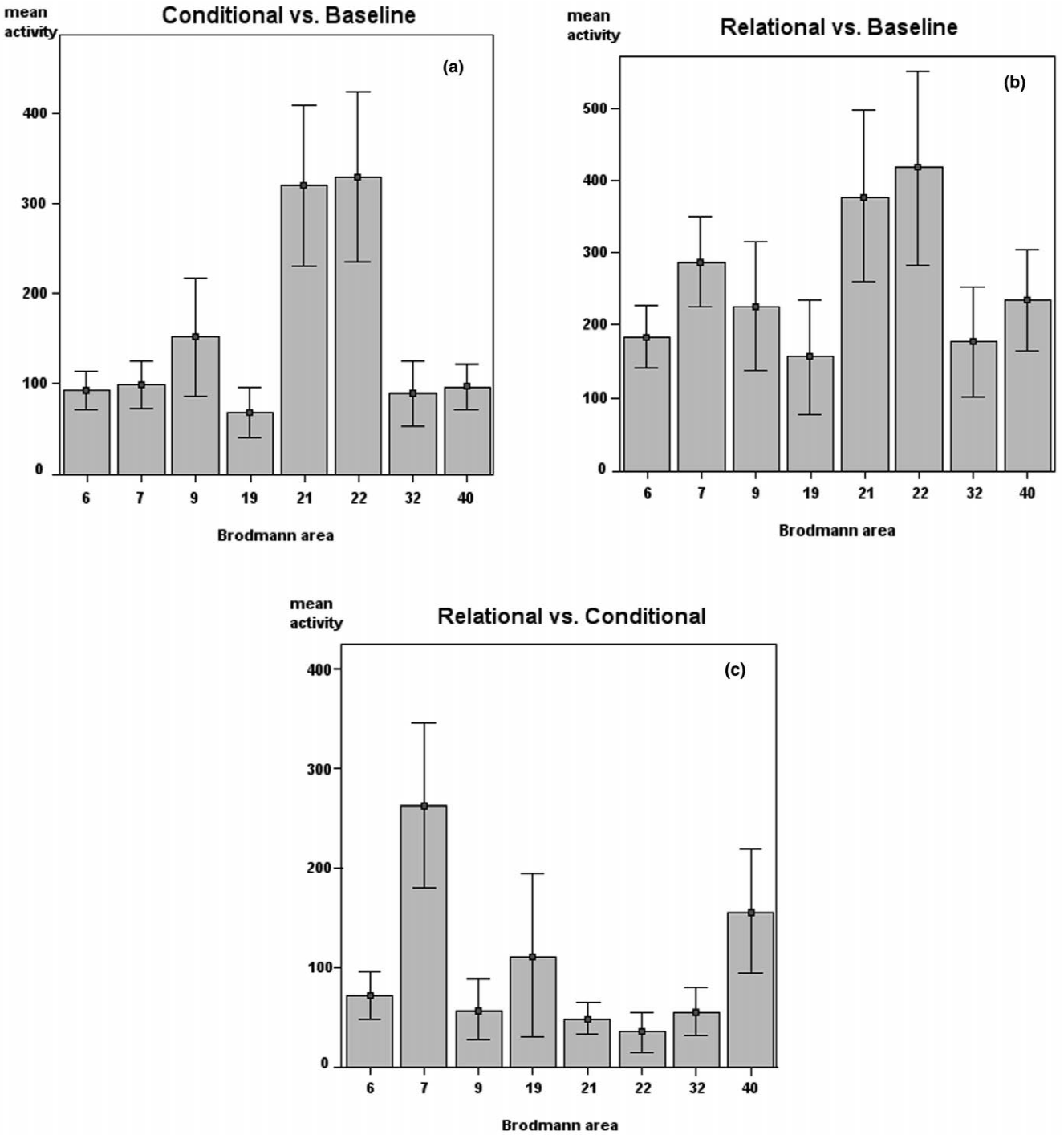

Fig. 1. Relative activation level of the analyzed ROIs (Brodmann areas 6, 7, 9, 19, 21, 22, 32, and 40) in the contrasts (a) conditional reasoning vs. baseline, (b) spatial reasoning vs. baseline, and (c) conditional vs. spatial reasoning. Values are indexed by the standard deviation of the T2* signal multiplied by the standardized correlation coefficient. The results are pooled for both hemispheres and show the mean values for 12 subjects.

reasoning activated the occipito-parietal pathway in the absence of any correlated visual input. Although this is an essential result for reasoning, it is supported by brain imaging studies on working memory and mental imagery. Reasoning is undoubtedly a process in which information must be maintained and manipulated. It is a widely shared assumption that these main functions of working memory are achieved by three subsystems: the phonological loop (PL) is responsible for verbal information, the visuo-spatial sketch pad (VSSP) handles and maintains spatial and/or visual information, and the central executive (CE) is described as a supervisor that is responsible for the coordination of the subsystems and the selection of appropriate reasoning and storage strategies [1,2]. The PL

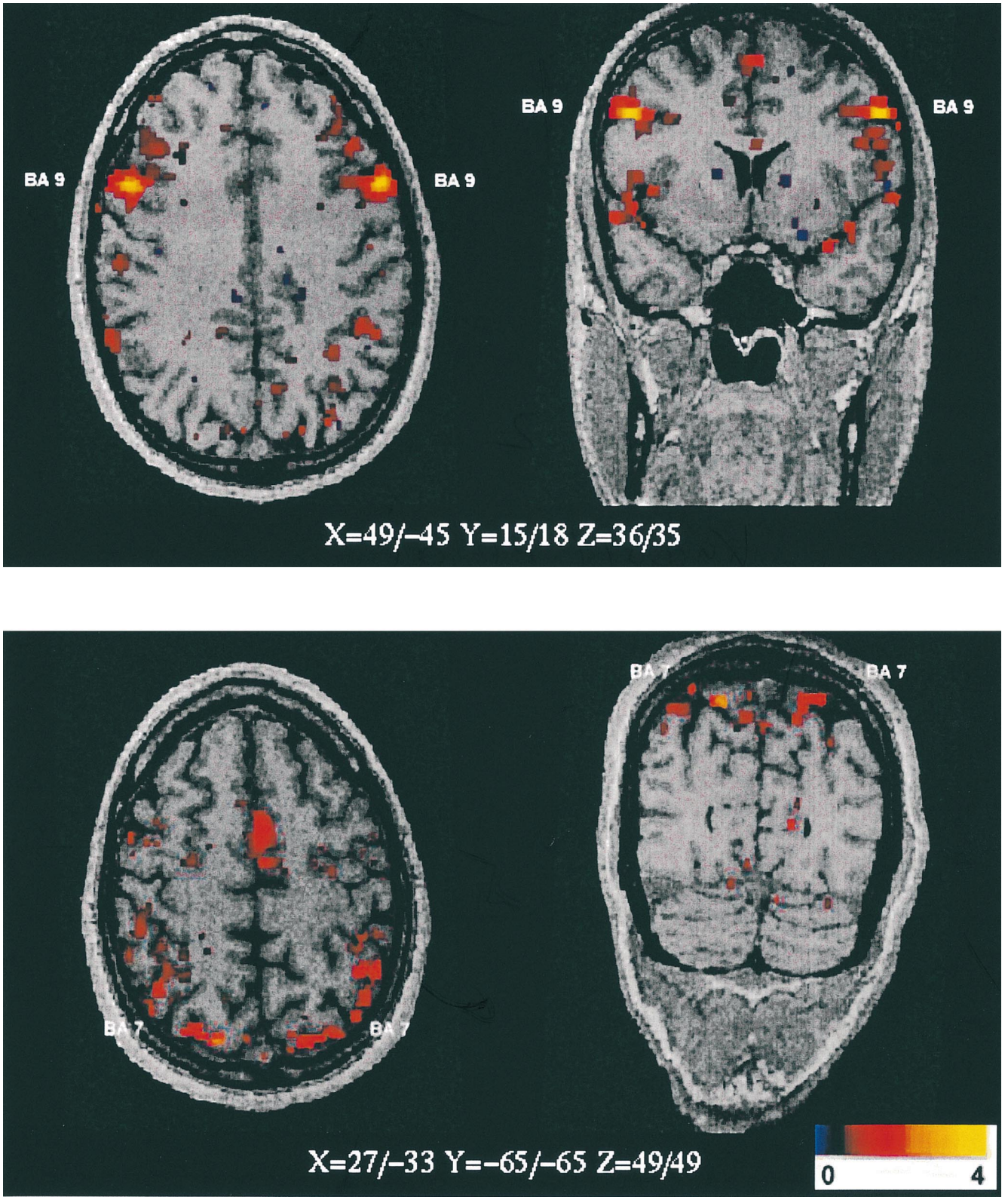

Fig. 2. Representative axial and coronal slices of one subject showing localization of activated ROIs in prefrontal (BA 9) and parietal (BA 7, 40) areas superimposed on the anatomical MRI data set. *Z*-score is indexed by the colorbar.

Table 1
Activated ROIs (anatomical localization and Brodmann's area together with mean Talairach coordinates of the center, separated for the left and right hemispheres) and *Z*-scores for the comparisons conditional reasoning vs. baseline, spatial reasoning vs. baseline, and spatial vs. conditional reasoning

Location	Mean Talairach coordinates			Mean *Z*-scores		
(Brodmann's area)	*x*	*y*	*z*	relational vs. baseline	conditional vs. baseline	relational vs. conditional
Frontal						
R medial frontal gyrus (6)	3 (±2)	−4 (±8)	57 (±6)	3.81 (±0.37)	3.16 (±0.56)	2.00 (±0.25)
L medial frontal gyrus (6)	−4 (±2)	−1 (±12)	54 (±6)	3.74 (±0.57)	3.09 (±0.46)	1.51 (±0.29)
R middle frontal gyrus (9)	49 (±3)	15 (±8)	36 (±3)	3.76 (±0.41)	3.18 (±0.20)	1.24 (±0.45)
L middle frontal gyrus (9)	−45 (±4)	18 (±16)	35 (±3)	3.87 (±0.40)	3.40 (±0.20)	1.19 (±0.27)
R cingulate gyrus (32)	4 (±3)	8 (±6)	43 (±3)	4.27 (±0.41)	3.04 (±0.18)	1.63 (±0.28)
L cingulate gyrus (32)	−6 (±2)	12 (±12)	41 (±6)	4.21 (±0.56)	3.07 (±0.22)	1.54 (±0.27)
Temporal						
R middle temporal gyrus (21)	59 (±3)	−38 (±8)	−1 (±4)	4.55 (±0.50)	4.60 (±0.48)	−0.40 (±0.87)
L middle temporal gyrus (21)	−60 (±5)	−35 (±10)	−1 (±2)	4.46 (±0.41)	4.37 (±0.44)	−0.27 (±0.60)
R superior temporal gyrus (22)	56 (±7)	−36 (±17)	8 (±5)	4.74 (±0.24)	4.73 (±0.22)	0.20 (±0.27)
L superior temporal gyrus (22)	−58 (±4)	−37 (±17)	8 (±5)	5.09 (±0.33)	4.79 (±0.27)	0.69 (±0.54)
Parietal						
R superior parietal gyrus (7)	27 (±6)	−65 (±7)	49 (±4)	3.38 (±0.51)	2.21 (±0.43)	2.33 (±0.56)
L superior parietal gyrus (7)	−33 (±7)	−65 (±8)	49 (±4)	3.55 (±0.60)	2.54 (±0.45)	2.31 (±0.59)
R precuneus (7)	5 (±3)	−69 (±5)	47 (±6)	3.33 (±0.54)	2.29 (±0.42)	2.15 (±0.38)
L precuneus (7)	−9 (±4)	−66 (±6)	48 (±6)	3.47 (±0.34)	2.66 (±0.42)	2.51 (±0.45)
R inferior parietal gyrus (40)	39 (±10)	−56 (±7)	39 (±9)	3.93 (±0.33)	2.93 (±0.57)	1.98 (±0.72)
L inferior parietal gyrus (40)	−37 (±8)	−55 (±7)	39 (±9)	4.03 (±0.20)	3.39 (±0.61)	1.77 (±0.47)
Occipital						
R middle occipital gyrus (19)	19 (±16)	−78 (±5)	33 (±7)	3.43 (±0.41)	2.60 (±0.58)	2.00 (±0.40)
L middle occipital gyrus (19)	−21 (±9)	−82 (±7)	31 (±9)	3.41 (±0.37)	2.46 (±0.60)	1.82 (±0.47)

Standard deviations (±) for Talairach coordinates and *Z*-scores are presented in parentheses.

and the VSSP can be further divided into storage and maintenance subsystems [1,45]. Besides multiple behavioral experiments supporting this theoretical framework, there are also studies on the cortical correlates of the three subsystems, which examine the degree to which they are involved in different cognitive functions [10,12,64]. According to these studies, spatial working memory tasks evoke regions of the parietal cortex, which are usually called the dorsal route or 'where-pathway' of vision [68] and working memory [63,67]. Multiple PET and fMRI studies reported brain activity related to spatial memory tasks in the parietal cortex, in particular in BA 7 and 40 (for review, see Ref. [10]).

One can object that reasoning differs in a number of important aspects from working memory and therefore does not rely on the same brain regions. Such a position, however, is challenged by behavioral studies that recently investigated the role of the working memory subsystems in different sorts of reasoning. The overall pattern of results from these experiments is that the VSSP is involved in almost all kinds of reasoning, whereas only weak evidence for the involvement of the PL was obtained [31,35,36,69].

Other imaging studies, however, failed to find activation in the parietal cortex during reasoning and, hence, claim that human reasoning is based on a mental logic consisting of inference rules represented in a language-like format [19,20]. Some authors argued that rules for reasoning need not be literally 'sentential' in nature, but rather can be based on more abstract propositions [64]. However, the key assertion of the theory is a repertoire of inference rules which are derived from general knowledge and refer to sentential connectives such as 'if' and 'then', and quantifiers like 'all' and 'some'. The language-based rules are used to solve inference problems by introducing and eliminating sentential connectives [6,55]. However, the data reported here do not support this sentential account of reasoning. Instead, the obtained activation in a bilateral occipito-parietal network provide evidence that reasoning is a cognitive process in which spatially organized mental models are used for reasoning [26,29]. In general, the mental model theory postulates that reasoners construct spatial mental models, inspect them to find a putative conclusion, and then search for counterexamples that satisfy the premises but refute the putative conclusion. If such a counterexample is not found, the conclusion is valid. In contrast to visual mental images, mental models are a form of representation that can be spatial but more abstract [28]. Mental models represent information in a multi-dimensional array that maintains ordinal and topological properties and avoids distracting details. The spatial representation is processed using primitive functions that transform and inspect the spatial array. Moreover, a multi-

dimensional array is able to depict spatial and topological relations as well as non-spatial dimensions, such as kinship.

However, the fact that the activity in parietal regions and the visual association cortex (BA 19) was not accompanied by primary visual cortex activation also has implications for the visual imagery theory of reasoning. According to Kosslyn's theory, visual mental images are quasi-pictures represented in a specific medium called the visual buffer. This subsystem is claimed to correspond to the primary visual cortex. In general, theories of visual mental imagery in reasoning propose three types of processes in the visual buffer: the generation process forms a visual image, the transformation process (for example, rotation, translation, reduction in size, etc.) modifies the image or views it from a certain perspective, and the inspection process retrieves information from this representation [5,41,59].

On the one hand, the strictest neuro-anatomical hypothesis that reasoning evokes activity in the primary visual cortex [41] is not supported by the present data. On the other hand, other brain imaging studies indicate that mental imagery tasks do not necessarily involve early visual areas. In a previous fMRI study of our group [37], for instance, we obtained behavioral data which were in agreement with the imagery literature in cognitive psychology, but nevertheless did not find activation in the primary visual cortex. Instead, activation was found in areas similar to the present study—in the inferior and superior parietal cortex and the visual association cortex. Similar results are reported in Roland and Gulyas [56], Mellet et al. [46,47], and D'Esposito [11]. Another noteworthy point is that Kosslyn [41] postulates that there are distinguishable cortical correlates for the processing of coordinate (metric) spatial information (and for visual image generation) and the processing of categorical spatial information (e.g. left vs. right, below vs. above). Given that our tasks did not involve metrical information, other tasks that involve such information may activate other brain regions.

4.2. Prefrontal areas and cingulate gyrus activation

Not only the occipito-parietal pathway is involved in visual and spatial working memory, but also prefrontal cortical areas. Baker et al. [3] have shown that prefrontal areas play a role in imagery and visuo-spatial working memory. In a study by D'Esposito et al. [10], portions of the supplementary motor area, corresponding to BA 6, appeared to play a role in the spatial encoding in working memory. Smith and Jonides [62] argue that the occipito-parietal route is primarily responsible for storage of spatial information, while the maintenance component is primarily localized in the prefrontal cortex (with a right-hemisphere prevalence), including some premotor areas and the supplementary motor area (SMA).

The activity in portions of the middle frontal gyrus, corresponding to BA 9, reflects that reasoning involves the active manipulation and inspection of information in working memory. Petrides [50] argues that BA 9 (together with BA 46) is related to executive functions and postulates that BA 9 is typically involved in cognitive processes 'when several pieces of information in working memory need to be monitored and manipulated' [49, p. 90]. Moreover, several behavioral studies demonstrated that the central executive is involved in almost all kinds of reasoning [31,66,69].

The activity in the anterior cingulate gyrus (BA 32) is in agreement with other studies on reasoning that likewise found activation in this area [19,20]. Activity in the cingulate gyrus can be evoked by different cognitive processes, but there is no generally accepted theory about its main functions. Some researchers argue that the anterior cingulate gyrus is related to attention and to the initiation of actions [52], whereas others assume that the anterior cingulate gyrus is responsible for the inhibition of irrelevant information in working memory (for instance in Stroop tasks; [18]).

In general, the question of how complex reasoning problems evoke prefrontal cortical regions needs a more detailed experimental setting. For the present research question it was feasible to use the fixation-cross as a baseline condition, since we were primarily interested in parietal and occipital activation. However, for a detailed analysis of activation in brain regions related to executive functions, a baseline condition that is more similar to the experimental conditions is desirable.

5. Conclusion

The aim of the present study was to investigate the neural correlates of human deductive reasoning. From the different sorts of deductive reasoning we selected two: relational and conditional reasoning. As proposed by several authors, we identified the spatial accounts of reasoning with (right) parietal activity, mental proof theories with activity in (left) temporal regions, and the visual account with activation of the primary visual cortex.

The present study yielded a surprising result: as a neural correlate of two basic kinds of reasoning, we identified a bilateral occipitoparietal–frontal network distributed over parts of the prefrontal cortex and the cingulate gyrus, the inferior and superior parietal cortex, the precuneus, and the visual association cortex. These results provide evidence that deductive reasoning is based on spatial representations and processes, and they appear to corroborate the mental model theory of reasoning. Sentential accounts, such as the theory of mental proof, are not supported by the present data. The relation between the reported results and the visual imagery theory of reasoning is not clear. On the one hand, we did not find activation in the primary visual cortex. On the other hand, increased activation occurred in

the visual association cortex and parietal regions, although there was no correlated visual input.

Acknowledgements

The research was supported the German National Research Foundation (Deutsche Forschungsgemeinschaft; DFG) under contract numbers Str 301/5-2 (MeMoSpace project), Kn 465/2-1, and Kn 465/2-3 (WorkSpace project).

References

[1] A.D. Baddeley, Working Memory, Oxford University Press, Oxford, 1986.
[2] A.D. Baddeley, G. Hitch, Working memory, in: G.H. Bower (Ed.), The Psychology of Learning and Motivation, Vol. 8, Academic Press, New York, 1974, pp. 47–89.
[3] S.C. Baker, C.D. Frith, R.S. Frackowiak, R.J. Dolan, Active representation of shape and spatial location in man, Cereb. Cortex 6 (1996) 612–619.
[4] P.A. Bandettini, A. Jesmanowicz, E.C. Wong, J.S. Hyde, Processing strategies for time-course data sets in functional MRI of the human brain, Magn. Reson. Med. 30 (1993) 161–173.
[5] B. Berendt, Explaining preferred mental models in Allen inferences with a metrical model of imagery, in: Proceedings of the 18th Annual Conference of the Cognitive Science Society, Erlbaum, Mahwah, NJ, 1996, pp. 489–494.
[6] M.D.S. Braine, D.P. O'Brein (Eds.), Mental Logic, Erlbaum, Mahwah, NJ, 1998.
[7] A. Caramazza, J. Gordon, E.B. Zurif, D. DeLuca, Right-hemispheric damage and verbal problem solving behavior, Brain 3 (1976) 41–46.
[8] R.W. Cox, AFNI: software for analysis and visualization of functional magnetic resonance neuroimage, Comput. Biomed. Res. 29 (1996) 162–173.
[9] V.L. Deglin, M. Kinsbourne, Divergent thinking styles of the hemispheres: How syllogisms are solved during transitory hemisphere suppression, Brain Cogn. 31 (1996) 285–307.
[10] M. D'Esposito, G.K. Aguirre, E. Zarahn, D. Ballard, R.K. Shin, J. Lease, Functional MRI studies of spatial and nonspatial working memory, Cogn. Brain Res. 7 (1998) 1–13.
[11] M. D'Esposito, J.A. Detre, G.K. Aguirre, M. Stallcup, D.C. Alsop, L.J. Tippet, M.J. Farah, A functional MRI study of mental image generation, Neuropsychologia 35 (1997) 725–730.
[12] M. D'Esposito, J.A. Detre, D.C. Alsop, R.K. Shin, S. Atlas, M. Grossman, The neural basis of the central executive system of working memory, Nature 378 (1995) 279–281.
[13] J.St.-B.T. Evans, S.T. Newstead, R.M.J. Byrne, Human Reasoning, Erlbaum, Hove, UK, 1993.
[14] R.A. Finke, Principles of Mental Imagery, MIT Press, Cambridge, MA, 1989.
[15] K.J. Friston, A.P. Holmes, J.B. Poline, P.J. Grasby, S.C.R. Williams, R.S.J. Frackowiak, R. Turner, Analysis of fMRI time series revisited, NeuroImage 2 (1995) 45–53.
[16] M.S. Gazzaniga, The Social Brain, Basic Books, New York, 1985.
[17] G.C. Geminiani, M. Bucciarelli, Deductive reasoning in right-brain damaged, in: Proceedings of the 17th Annual Conference of the Cognitive Science Society, Erlbaum, Mahwah, NJ, 1995, pp. 386–391.
[18] M.S. George, T.A. Ketter, P.I. Parekh, N. Rosinsky, H. Ring, B.J. Casey, M.R. Trimble, B. Horwitz, P. Herscovitch, S.M. Post, An H2150 PET study on the stroop and the emotional stroop, Hum. Brain Mapp. 1 (1994) 194–209.
[19] V. Goel, B. Gold, S. Kapur, S. Houle, The seats of reason: a localization study of deductive and inductive reasoning using PET (O15) blood flow technique, NeuroReport 8 (1997) 1305–1310.
[20] V. Goel, B. Gold, S. Kapur, S. Houle, Neuroanatomical correlates of human reasoning, J. Cogn. Neurosci. 10 (1998) 293–302.
[21] J.I. Glasgow, D. Papadias, Computational imagery, Cogn. Sci. 16 (1992) 355–394.
[22] J. Glasgow, N.H. Narayanan, B. Chandrasekaran (Eds.), Diagrammatic Reasoning, AAAI Press, Cambridge, 1995.
[23] C. Hagen, C. Schlieder, M. Knauff, R. Rauh, G. Strube, A cognitive modelling of preferred mental models, 1998. Online version accessible on http://www.iig.uni-freiburg.de/cognition/members/hagen/demo/mm01.html
[24] G. Hagert, Modeling mental models: Experiments in cognitive modeling of spatial reasoning, in: T. O'Shea (Ed.), Advances in Artificial Intelligence, North-Holland, Amsterdam, 1984, pp. 179–188.
[25] M.K. Johnson, C.L. Raye, Reality monitoring, Psychol. Rev. 88 (1981) 67–85.
[26] P.N. Johnson-Laird, Mental Models, Cambridge University Press, Cambridge, 1983.
[27] P.N. Johnson-Laird, Mental models, deductive reasoning, and the brain, in: M.S. Gazzaniga (Ed.), The Cognitive Neurosciences, MIT Press, Cambridge, MA, 1995, pp. 999–1008.
[28] P.N. Johnson-Laird, Imagery, vizualization, and thinking, in: J. Hochberg (Ed.), Perception and Cognition at Century's End, Academic Press, San Diego, CA, 1998, pp. 441–467.
[29] P.N. Johnson-Laird, R. Byrne, Deduction, Erlbaum, Hove, UK, 1991.
[30] J. Kassubek, K. Schmidtke, H. Kimmig, C.H. Lucking, M.W. Greenlee, Changes in cortical activation during mirror reading before and after training: an fMRI study of procedural learning, Cogn. Brain Res. 10 (2001) 207–217.
[31] K.C. Klauer, R. Stegmaier, T. Meiser, Working memory involvement in propositional and spatial reasoning, Thinking Reasoning 3 (1997) 9–47.
[32] M. Knauff, The cognitive adequacy of Allen's interval calculus for qualitative spatial representation and reasoning, Spatial Cogn. Comput. 1 (1999) 261–290.
[33] M. Knauff, P.N. Johnson-Laird, Visual and spatial representations in spatial reasoning, in: Proceedings of the 22nd Annual Conference of the Cognitive Science Society, Erlbaum, Mahwah, NJ, 2000, pp. 759–765.
[34] M. Knauff, P.N. Johnson-Laird, Visual imagery can impede reasoning, (2001) submitted for publication.
[35] M. Knauff, C. Jola, G. Strube, Spatial reasoning: no need for visual information, in: D. Montello et al. (Ed.), Spatial Information Theory, Springer, New York, 2001, pp. 447–457.
[36] M. Knauff, C. Jola, G. Strube, R. Rauh, C. Schlieder, Visuo-spatial working memory involvement in spatial reasoning, (2001) submitted for publication.
[37] M. Knauff, J. Kassubek, T. Mulack, M.W. Greenlee, Cortical activation evoked by visual mental imagery as measured by functional MRI, NeuroReport 11 (2000) 3957–3962.
[38] M. Knauff, R. Rauh, C. Schlieder, Preferred mental models in qualitative spatial reasoning: A cognitive assessment of Allen's calculus, in: Proceedings of the 17th Annual Conference of the Cognitive Science Society, Erlbaum, Mahwah, NJ, 1995, pp. 200–205.
[39] M. Knauff, R. Rauh, C. Schlieder, G. Strube, Mental models in spatial reasoning, in: C. Freksa, C. Habel, K.F. Wender (Eds.), Spatial Cognition: An Interdisciplinary Approach To Representing and Processing Spatial Knowledge, Springer, Berlin, 1998, pp. 267–291.
[40] S.M. Kosslyn, Image and Mind, Harvard University Press, Cambridge, MA, 1980.

[41] S.M. Kosslyn, Image and Brain, MIT Press, Cambridge, MA, 1994.
[42] S.M. Kosslyn, N.M. Alpert, W.L. Thompson, V. Maljkovic, S.B. Weise, C.F. Chabris, S.E. Hamilton, S.L. Rauch, F.S. Buonanno, Visual mental imagery activates topographically organized visual cortex: PET investigations, J. Cogn. Neurosci. 5 (1993) 263–287.
[43] S.M. Kosslyn, A. Pascual-Leone, O. Felician, S. Camposano, J.P. Keenan, W.L. Thompson, G. Ganis, K.E. Sukel, N.M. Alpert, The role of area 17 in visual imagery: convergent evidence from PET and rTMS, Science 284 (1999) 167–170.
[44] S.M. Kosslyn, W.L. Thompson, N.M. Alpert, Neural systems shared by visual imagery and visual perception: a positron emission tomography study, NeuroImage 6 (1997) 320–334.
[45] R.H. Logie, Visuo-spatial Working Memory, Erlbaum, Hove, UK, 1995.
[46] E. Mellet, N. Tzourio, M. Denis, B. Mazoyer, A positron emission tomography study of visual and mental exploration, J. Cogn. Neurosci. 7 (1995) 433–445.
[47] E. Mellet, N. Tzourio, F. Crivello, M. Joliot, M. Denis, B. Mazoyer, Functional anatomy of spatial mental imagery generated from verbal instructions, J. Neurosci. 16 (1996) 6504–6512.
[48] D. Osherson, D. Perani, S. Cappa, T. Schnur, F. Grassi, F. Fazio, Distinct brain loci in deductive versus probabilistic reasoning, Neuropsychologia 36 (1998) 369–376.
[49] M. Petrides, Functional organization of the human frontal cortex for mnemonic processing. Evidence from neuroimaging studies, Ann. NY Acad. Sci. 15 (1995) 85–96.
[50] M. Petrides, The role of the mid-dorsolateral prefrontal cortex in working memory, Exp. Brain Res. 133 (2000) 44–54.
[51] S. Pigott, B. Milner, Capacity of visual short-term memory after unilateral frontal or anterior temporal-lobe resection, Neuropsychologia 32 (1994) 969–981.
[52] M.I. Posner, S.E. Peteron, The attention system in the human brain, Annu. Rev. Neurosci. 13 (1990) 25–42.
[53] V. Prabhakaran, J.A. Smith, J.E. Desmond, G.H. Glover, J.D. Gabrielli, Neural substrates of fluid reasoning: an fMRI study of neocortical activation during performance of the Raven's Progressive Matrices Test, Cogn. Psychol. 33 (1997) 43–63.
[54] D.E. Read, Solving deductive-reasoning problems after unilateral temporal lobectomy, Brain Lang. 12 (1981) 116–127.
[55] L.J. Rips, The Psychology of Proof, MIT Press, Cambridge, MA, 1994.
[56] P.E. Roland, B. Gulyas, Visual memory, visual imagery, and visual recognition of large field patterns by the human brain: functional anatomy by positron emission tomography, Cereb. Cortex 5 (1995) 79–93.
[57] P. Sabbah, G. Simond, O. Levrier, M. Habib, V. Trabaud, N. Murayama, B. Mazoyer, J.F. Briant, C. Raybaud, G. Salamon, Functional magnetic resonance imaging at 1.5 T during sensorimotor and cognitive tasks, Eur. J. Neurol. 35 (1995) 131–136.
[58] C. Schlieder, The construction of preferred mental models in reasoning with interval relations, in: G. Rickheit, C. Habel (Eds.), Mental Models in Discourse Processing and Reasoning, Elsevier, Amsterdam, 1999, pp. 333–357.
[59] C. Schlieder, B. Berendt, Mental model construction in spatial reasoning: A comparison of two computational theories, in: U. Schmid, J.F. Krems, F. Wysotzki (Eds.), Mind Modelling: A Cognitive Science Approach to Reasoning, Learning and Discovery, Pabst, Lengerich, 1998, pp. 133–162.
[60] R.N. Shepard, L.A. Cooper, Mental Images and Their Transformations, MIT Press, Cambridge, MA, 1982.
[61] A.T. Smith, M.W. Greenlee, K.D. Singh, F.K. Krõmer, J. Hennig, The processing of first- and second-order motion in human visual cortex assessed by fMRI, J. Neurosci. 18 (1998) 3816–3830, (see also: http://www.liv.ac.uk/mariarc/software.html.
[62] E.E. Smith, J. Jonides, Working memory: a view from neuroimaging, Cogn. Psychol. 1 (1997) 5–42.
[63] E.E. Smith, J. Jonides, R.A. Koeppe, E. Awh, E.H. Schuhmacher, S. Minoshima, Spatial versus object working memory: PET investigations, J. Cogn. Neurosci. 7 (1995) 337–356.
[64] K. Stenning, J. Oberlander, A cognitive theory of graphical and linguistic reasoning: Logic and implementation, Cogn. Sci. 19 (1995) 97–140.
[65] J. Talairach, P. Tournoux (Eds.), Co-Planar Atlas of the Human Brain: 3-Dimensional Proportional System, Thieme, Stuttgart, 1988.
[66] M. Toms, N. Morris, D. Ward, Working memory and conditional reasoning, Q. J. Exp. Psychol. A 46 (1993) 679–699.
[67] L.G. Ungerleider, Functional brain imaging studies of cortical mechanisms for memory, Science 270 (1996) 769–775.
[68] L.G. Ungerleider, M. Mishkin, Two cortical visual systems, in: D.J. Ingle, M.A. Goodale, R.J.W. Mansfield (Eds.), Analysis of Visual Behaviour, MIT Press, Cambridge, MA, 1982, pp. 549–586.
[69] A. Vandierendonck, G. De Vooght, Working memory constraints on linear reasoning with temporal and spatial contents, Q. J. Exp. Psychol. A 50 (1997) 803–820.